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CAREY, HANNAH V.

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University of California, Davis PH.D. 1983

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Foraging and Nutritional Ecology of Yellow-bellied Marmots in the White Mountains of California

By

HANNAH V. CAREY
B.S. (State University of New York, Binghamton) 1977
M.A. (University of California, Davis) 1980

DISSERTATION

Submitted in partial satisfaction of the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

Zoology

in the

GRADUATE DIVISION

of the

UNIVERSITY OF CALIFORNIA

DAVIS

Approved:

George W Salt

Committee in Charge

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Foraging and Nutritional Ecology of Yellow-bellied Marmots in the White Mountains of California

ABSTRACT

This research investigated some of the factors that influence nutrient acquisition and predator avoidance in the yellow-bellied marmot, Marmota flaviventris. The study was conducted in a meadow at 3650 m elevation in the White Mountains of California. In this region marmots are active from early May to mid September and hibernate the remainder of the year.

The marmots spent about 10% of their feeding time looking up, a behavior crucial for predator avoidance but one that reduces the rate of food intake. Marmots were more vigilant when alarm calls were emitted by conspecifics than in the absence of calls. Vigilance time was reduced when marmots fed in groups, and in areas with open vegetation and many safety burrows. These results suggest that the cost of antipredator behavior in reduced feeding rates may be minimized by adjusting the time spent in vigilance relative to the risk of predation.

Marmots preferred forbs over graminoids, particularly in the spring and early summer even though graminoids were more abundant in the habitat. Chemical analyses suggested that this preference is related to the forbs' lower fiber (cellulose) content and their higher concentrations of phosphorus, sodium and possibly protein. Seasonal changes in diet composition were noted which may reflect changes in food quality and in nutrient requirements of marmots.

Preference for foraging areas was positively correlated with food plant availability and negatively correlated with structural charac-

Preference for foraging areas was positively correlated with food plant availability and negatively correlated with structural characteristics of feeding areas that may restrict visual range. This preference may be interpreted as adaptive behavior balancing the simultaneous demands of food ingestion and predator avoidance.

Juvenile marmots spent more time in predator vigilance during foraging than did older animals, and were also more sensitive to the factors that influenced vigilance. Juveniles, and to a lesser extent adult females exhibited the strongest relationships between foraging area preferences and habitat characteristics. Although diet composition was not found to vary with age, juveniles may supplement their diets with additional nutrients such as protein and vitamins through ingestion of adult fecal material. Differences among age classes in the risks associated with predation and inadequate nutrition produce age-specific variations in foraging patterns.

ACKNOWLEDGEMENTS

I would like to extend my thanks to the following people and agencies for their support during my graduate career:

First, my major professor, Dr. Robert L. Rudd, has been a never-ending source of support, advice and friendship. My association with him has been and will continue to be a rewarding experience.

Earlier drafts of this thesis were greatly improved by the comments of my thesis committee: Drs. Robert Rudd, George Salt and Catherine Toft. Dr. Warren Holmes, Dr. John Wehausen, Dr. Martin Simon, Tim Stevens and Patrice Moore also provided valuable comments.

Many of the ideas presented here were formed through discussions with the Zoology Department´s Ecology Brown Bag Lunch Group. In particular, the help of Dr. William Rice was invaluable in the experimental design and statistical analysis of many parts of this study. Dr. Michael Miller of the UCD Statistical Consulting Lab also provided useful advice. Other members of the Zoology Department who shared ideas and friendship throughout my graduate career include Susan Sanders, Ted Beedy, Lisa Palermo, John Harris, Bruce Barnett, Aileen Kennedy, Ed West and Art Shapiro. Russ Davis was instrumental in my introduction to marmots and shared many stimulating discussions and special moments in the field during the early phases of the project.

No study such as this one could be carried out without the help of field companions. For assistance in the field I am very grateful to Russ Davis and my field assistants Laura Bond, Jerry Cook, Lisa Penwell, Ted Cunningham and Patrice Moore. In addition, the logistical support and friendship of staff and crewmembers of the White Mountain Research Station helped to make my experience in the White Mountians extremely productive and enjoyable. Tim Spira was a source of friendship and many stimulating discussions on alpine ecology and the simularities between marmots and gentians.

I am grateful to Dr. Brian Mulloney for making the preparation of this dissertation immeasureably easier; his words of encouragement and advice concerning future career goals are also very much appreciated.

The University of California, Davis supported much of this research and my expenses in graduate school through Intercampus Travel awards, a Graduate Research award, Graduate Fellowships and Teaching Assistantships. The following agencies also provided financial support for various aspects of this research: The White Mountain Research Station, The American Alpine Club, Sigma Xi, The Theodore Roosevelt Memorial Fund, The National Academy of Sciences, and American Women in Science.

Assistance in nutritional analyses was provided by the UCD Animal Science Nutrition Lab and the Forestry Sciences Lab, Corvallis.

Very special thanks go to two good friends and colleagues, Patrice Moore and Martin Simon, who generously offered their advice and assistance in many aspects of the design, execution and analysis of this study. To them, I extend my deep gratitude.

This thesis is dedicated to my dear parents, wthout whose continual support, friendship and love this dissertation would never have been completed.

INTRODUCTION

Food acquisition is an important concern for all animals. The fulfillment of this requirement has far-reaching effects on many characteristics of animal populations, including such things as social organization, dispersal patterns, life history parameters and community structure. In understanding feeding and the selective forces that have contributed to the diversity of feeding patterns that exist, it is essential to have some knowledge of the rewards and constraints that influence the feeding behavior of a species in a particular environment.

Yellow-bellied marmots (Marmota flaviventris) are medium-sized rodents found in mountainous regions of western North America. Two aspects of the biology of these animals are of prime importance in understanding their foraging ecology. First, marmots are nonruminant herbivores which means that their relatively low quality plant foods are not subject to the specialized fermentation systems possessed by many ungulates such as cattle and sheep. Second, marmots are deep hibernators. Hibernation, through a reduction of body temperature and metabolic rate minimizes energy expenditure during times when food resources are scarce and climatic conditions extreme. However, without adequate energy reserves in the form of fat deposited during the active season, winter mortality is inevitable. This thesis examines some of the ways that these two aspects of marmot biology - herbivory and hibernation - influence the foraging ecology of this species.

In chapter 1 I examine the influence of predation risk on foraging behavior. Vigilance during foraging reduces the probability of undetected predator attack. However, it also imposes a cost on foraging by reducing the rate of food ingestion. This section identifies this cost and discusses some of the factors that modify the time marmots invest in vigilance behavior.

Chapter 2 focuses on food quantity and quality as determinants of nutrient intake. This portion of the study was designed to determine if the composition of the marmot diet reflects preference for certain types of plants or if intake is due solely to the availability of plants in the environment. I also examined the nutritional basis of food preference as well as temporal variations in diet composition that might result from changes in food availability as well as changing nutritional demands during the the active season.

Both food resources and predator avoidance are incorporated in Chapter 3, which discusses the marmots' use of foraging areas. The choice of feeding areas may not only be directed by food availability; because a forager is often more vulnerable to predation while feeding, predator avoidance should also influence the movements of a foraging animal. Chapter 3 outlines the extent to which marmots respond to habitat qualities reflecting the demands of both feeding and predator avoidance.

An underlying theme throughout this thesis is age differences in foraging behavior. I hypothesized early in the study that the constraints imposed on adult hibernators may exert even stronger demands on juveniles, the age class most vulnerable to a variety of mortality factors. Indeed, the age-specific variations in feeding ecology that were found for the marmots highlight most if not all of the important conclusions that emerged from my work.

The appendixes to this thesis supply information on the activity patterns of the marmots studied during the project. The data found therein supplement those in Chapters 1-3 and provide supporting evidence to some of the conclusions made.

CHAPTER 1

The Influence of Predation Risk on the Foraging Behavior of Yellow-bellied Marmots

ABSTRACT

This study investigated the influence of predator vigilance on the feeding behavior of yellow-bellied marmots (*Marmota flaviventris*) in the White Mountains of California. Marmots spent 10.2% of their foraging time looking up, a behavior which is necessary for predator avoidance but reduces the rate of food intake. More time was spent looking up when alarm calls were emitted by conspecifics than in the absence of calls. Vigilance time was reduced when marmots fed in groups, and in areas with many safety burrows and open vegetation. These results suggest that the cost of antipredator behavior in reduced feeding rates may be minimized by adjusting the time spent in vigilance relative to the risk of predation. Juveniles and yearlings spent more time looking up while feeding than did adults. Juveniles also appeared to be more sensitive to the factors that influenced vigilance than were older animals, which may be due to the greater nutritional demands of young, growing animals coupled with a higher susceptibility to predation. The importance of behaviors that reduce the cost/benefit ratio of vigilance during foraging may lie in the selective value of attaining adequate fat stores as rapidly as possible during the hibernator's active season.

INTRODUCTION

Cost/benefit analysis has been used in recent years to explain the foraging patterns observed among animals (Covich 1976). The benefit of foraging seems straightforward - the acquisition of energy and/or nutrients which allows individuals to survive and reproduce. The costs associated with foraging are more varied and less well understood. They include thermoregulatory stress (Belovsky 1981, Dugan 1982), energetic drain (Karasov 1981), loss of territory (Myers et al. 1979a, Caraco et al. 1980), reduction of food supply for offspring (Barash 1980) and vulnerability to predation (Pulliam 1973).

The risk of predation while foraging has been studied in a variety of animals including birds (Powell 1974, Bertram 1980, Burger 1982), ungulates (Jarman 1974, Berger 1978, Underwood 1982, Lipetz and Bekoff 1982), insects (Sih 1982), and rodents (Barash 1973, Holmes 1979, Hoogland 1981). Vigilance, i.e., scanning the environment for potential predators, has played a central role in many of these investigations. Assessment of the adaptive value of antipredator behavior to a foraging animal must include some measure of its potential costs (Sih 1980b). The demonstration of a loss in individual fitness due to vigilance may be the ultimate measure of this cost. However, it is often very difficult to obtain data of this sort (Hoogland 1979). An indirect way to assess the cost of antipredator behavior is to measure the decrease in feeding rate associated with vigilance, with the assumption that looking for predators and ingesting food are mutually exclusive or at least conflicting activities. To the extent that a decrease in feeding rate reduces fitness, behaviors that minimize the cost/benefit ratio of vigilance would be favored by natural selection.

There are at least three ways by which an individual can reduce vigilance time and thereby increase feeding time without increasing its risk of predation:

(1) Forage in areas that contain a high density of refuges (e.g., burrows) so that escape distance is small. Less time can be spent in initial predator detection because the time needed to escape once a predator is sighted is reduced.

(2) Forage in areas that offer a wide sensory range in which to detect an approaching predator (e.g., in open vegetation). Vigilance time can be reduced in such areas because more time is available for escape once a predator is sighted than would be if the predator was first seen when it was within striking distance.

(3) Forage near other animals that are also watching for predators. Foraging in groups may increase the probability that a predator will be sighted as early as possible, assuming that individuals are sensitive to antipredator signals produced by other animals in the area.

Variability in vigilance time may also be due to differential susceptibility to predation among individuals (Stein and Magnuson 1976, Sih 1982). For example, young animals are generally more vulnerable to predation than are adults; behavioral adjustments in response to predation risk may therefore be more valuable to juveniles. However, the additional dependence on nutrient intake for growth may make compromises between foraging and predator avoidance especially critical for juveniles.

This study examined the effect of predator vigilance on the feeding behavior of yellow-bellied marmots (Marmota flaviventris). These rodents (family Sciuridae) are deep hibernators that are active 4-5 months per year; during this time they must mate, bear young and deposit enough body fat to sustain them through the next hibernation period. The short season of activity thus places strict time constraints on feeding to accomplish these goals. Antipredator behavior by marmots is easily observed. As in many other ground-dwelling sciurids, marmots vocalize when a predator is sighted, which may alert other marmots to potential danger. Visual alarms (Hoogland 1981) are also common and occur when a marmot makes a sudden run to a burrow or rock perch in response to a perceived threat of predation. Other marmots may respond to this movement and either run to a burrow or stay in the same place and increase their level of vigilance. In this paper I will show that vigilance imposes a cost on foraging marmots, and that the cost varies with social, environmental and age-related factors that alter predation risk.

MATERIALS AND METHODS

Study area

The study was conducted in MacAfee Meadow (37 35′N, 118 12′W) at 3650 meters elevation in the White Mountains of California during the summers of 1980-1982. The data presented here were collected in 1982, and are based on 20 observation hours of one colony of marmots. ′Colony′ was defined as those marmots having full and exclusive use of foraging areas surrounding a common sleeping burrow area. In 1982, the colony was composed of 26 individuals - 15 juveniles (animals in their first summer), 5 yearlings (animals in their second summer), and 6 adults (animals older than 2 years). The colony resided around a rock outcrop on the meadow floor which is dominated by sedges (Carex spp.) and rushes (Juncus spp.). The marmots foraged as far as 300 meters from their burrows and ranged mainly on the surrounding slopes which contain a higher diverity of plants than does the meadow floor. Additional details on the animals, vegetation and study site are in Carey (1983).

Behavioral observations

Data collection began on 27 June, when juveniles first began appearing above-ground from their natal burrows, and terminated on 9 September, 2 weeks before the last individuals had gone underground for the winter. Most animals were marked for long-range visual identification with Nyanzol D fur dye. Unmarked animals were categorized as juveniles, yearlings or adults on the basis of body size and shape.

Individual foraging marmots were chosen randomly and observed for one minute sample periods during which the total time spent looking up was recorded. Looking-up time was later converted to percent of the minute-long sample for statistical analysis. The time not spent looking up during each sample was assumed to be spent in feeding or feeding-related activities such as searching for food. Observations were made from a tower (5.5 m) located at one edge of the colony's home range during the early morning and late afternoon when foraging activity is greatest.

For each sample period I recorded the age of the focal animal, the foraging group size (marmots within 15 meters of the focal animal) and the occurrence of alarm calls during the sample minute as well as any occurring during the preceding minute (none, 1-5 calls, more than 5 calls). The individual was located in one of 11 designated foraging areas that were based on vegetation type, structural characteristics (e.g., percent of rock cover) and distance from the sleeping burrows (see Carey 1983 for further descriptions of foraging areas). Safety burrow density (including sleeping burrows) and the mean vegetation volume in each area were determined. The latter variable was calculated by determining the mean height of all plants that extended 5 cm or higher above the ground surface and multiplying this value by the plant cover, thus providing a measure of the openness of an area. Most of the plants that met the height criterion were not preferred food plants (Carey 1983).

Five to 7 samples were collected for each individual in a given location within a 10-minute observation period. Mean values for each variable were calculated for the 5-7 samples and used as the data points in the analyses. Sets of observations on the same individual were always separated by at least one and more often 6 hours. Samples collected from the same individual on the same day always involved different locations. The data were examined prior to analysis for evidence of high degrees of intra-individual variability that might obscure the results. Since none was found and the restrictions on data collection outlined above were applied, I assumed that the means of each set of samples were independent and thus amenable to statistical analysis.

A single adult marmot was observed at close range for one minute in order to obtain an approximate measure of the maximum potential food ingestion rate. Foraging was continuous during this time with no look-up periods. The number of blades of grass ingested during 6 10-second intervals was counted and the number of blades making up one gram of grass (dry weight) was determined. These observations allowed an estimate of the potential dry weight of grass that could be ingested per minute by an adult marmot.

Statistical analysis

Linear correlation and multiple regression analyses were used to determine the factors that influenced vigilance behavior. The dependent variable was the percent of time spent looking up per minute. Independent variables were age of the focal animal, foraging group size, alarm call frequency, density of safety burrows in the foraging area, and mean vegetation volume of the area. Multiple regressions were run using the BMDP9R statistical program (Dixon 1981) which chooses the best subset of predictor variables based on a specified criterion, which for this analysis was the smallest value of Mallows′ Cp (Daniel and Wood 1971). All significance levels ($P \leq .05$) resulted from two-tailed significance tests; means are reported as $\bar{x}(\pm SE)$.

RESULTS

The cost of vigilance

One hundred and five observation means representing 677 minute-long samples were obtained. Eighty-four of these observation means came from 19 known individuals (8 juveniles, 6 yearlings and 5 adults), while the remaining 21 were from animals of known age (11 juveniles, 7 yearlings, 3 adults) but unknown identities.

The marmots spent 10.2% (± 0.5%) of their foraging time looking up (all ages combined). Since marmots were sometimes observed to forage continuously for up to 5 minutes without raising their heads, I assumed that the time spent looking up did indeed detract from the maximum food ingestion rate. Although marmots occasionally chewed while looking up, in most cases looking up and any type of feeding-related behavior were separate activities.

The adult marmot whose feeding was observed in detail ingested 0.38 grams dry weight of grass per minute. Based on this estimate of maximum feeding rate, a 10% time investment in vigilance behavior results in a potential loss of 0.04 grams dry weight of grass for each minute of foraging. The marmots in this study spent approximately 3.6 hours per day feeding (Carey 1983); an adult marmot can therefore potentially ingest 82.1 grams dry weight of grass per day. Vigilance behavior reduces this intake by 1.4 grams dry weight of grass per hour or 8.2 grams dry weight per day.

Factors influencing vigilance behavior

The results of the multiple regression analysis on the 105 observation means indicate that the percent of time spent looking up was significantly related to foraging group size, alarm call occurrence, and age of the animal. The regression model including these variables was significant ($F = 10.13$, $P \leq .0001$) and accounted for 23% of the variability in the data. However, safety burrow density and vegetation volume also appear to have influenced vigilance behavior (Table 1).

The occurrence of alarm calls had a positive effect on vigilance time. The mean percent of time spent looking up when calls were heard was 12.1% (±0.7%); this dropped to 8.3% (±0.9%) in the absence of calls.

The size of the foraging group had a strong negative effect on vigilance: marmots spent less time looking up when foraging near other marmots (Figure 1). Solitary foragers spent 12.7% (±0.9%) of their feeding time looking up for predators; this time was reduced to 8.6% (±0.6%) for animals foraging near at least one other marmot and further reduced to 5.1% (±0.9%) for groups of 5 or more, a 60% reduction compared with solitary foragers. The reason for the increase in mean looking-up time for group size 4 is unknown, although differences among group sizes of 2, 3 and 4 are slight. Closer examination of samples collected for group size 4 revealed no relationships between mean vigilance time and any other independent variables measured.

The effect of age on vigilance was examined using data collected on solitary foragers to remove the effect of group size. Although vigilance time did not differ significantly between juveniles and yearlings, the behavior of both groups of young animals was distinct from that of adults (Table 2). In addition, when the data were categorized by age the correlations between vigilance time and the independent variables indicate that it was largely the behavior of juveniles, and to a lesser degree, yearlings that accounted for the significant values in the entire data set (Table 1).

Multiple regression analysis was performed on data obtained only from juveniles to further clarify the factors that influenced vigilance time. The results (Table 3) include all four factors (except age) in the best-fit regression model, which accounts for 52% of the variability in the data. Due to intercorrelation between some of the independent variables (multicollinearity), the relative magnitude of each of the variables′ effects (contribution to R^2) could only be estimated. However, multicollinearity tends to inflate the variance of regression coefficients, thereby making statistically significant t-values more difficult to obtain (Neter and Wasserman 1974). The significance value of each of the independent variables is therefore a conservative estimate of its effect on the vigilance behavior of juveniles.

Foraging group size and the occurrence of alarm calls were influential in the amount of time juveniles spent looking up while foraging. In addition, safety burrow density appeared to modify the amount of time juveniles invested in vigilance. Juveniles spent less time looking up when feeding in areas of higher safety burrow density (Figure 2), although mean vigilance time did not appear to change beyond burrow densities of 6 per 1000 m^2. Vigilance behavior was not detectably different when safety burrows are distinguished from sleeping burrows. The mean vigilance time of juveniles in the 2 areas that contained sleeping burrows was not significantly different from the mean value over all areas (17.1% ±1.7% vs. 15.8% ±1.2%, P>.05).

Vegetation volume was also included in the regression model on vigilance time of juveniles. Juveniles spent more time looking up in areas of high vegetation volume. Mean vigilance times differed significantly among areas with low, medium and high volume (7.6%, 14.5%, and 16.8% respectively; ANOVA, F=16.6, df=2, P=.0001). This habitat characteristic appears to be the least important of the predictor variables (Table 3).

DISCUSSION

The results of this study suggest that vigilance behavior of foraging yellow-bellied marmots varies with the level of predation risk perceived by a marmot in a given situation. Adjustments in antipredator behavior of other sciurid rodents as a function of risk have been described in *Spermophilus columbianus* (Betts 1976), *Spermophilus beecheyi* (Leger et al. 1979), *Spermophilus beldingi* (Robinson 1980) and *Marmota caligata* (Holmes 1979). Although experimental release of live or model predators in the vicinity of foraging marmots would be needed for a direct test of this hypothesis (e.g., Noyes and Holmes 1979), marmot responses to the variety of foraging situations examined in this study provide strong indirect evidence for the vigilance-risk conclusion. Those factors that appear to influence marmot vigilance behavior during foraging will be considered below.

Age

Young marmots (juveniles and yearlings) spent more time looking up when foraging than did adults. The same was found by Holmes (1979) for Alaskan hoary marmots. Naive, young animals of a number of species are less able to distinguish actual predators from harmless species and to accurately assess the type of alarm calls emitted by conspecifics (Robinson 1981, Seyfarth and Cheney 1980). Noyes and Holmes (unpublished data, cited in Holmes 1979) showed that adult hoary marmots in Washington State appeared to detect the presence of a model golden eagle (Aquila chrysaetos) significantly sooner than did juveniles. Consequently, until a juvenile can increase its antipredator abilities, either through direct experience or by watching more experienced animals, it is under a higher level of predation risk than are adults. In this study, the frequency of predators hunting in the study area increased dramatically after juveniles first emerged aboveground in early July (pers. observ.) which may also indicate heavier predation pressure on this age class.

Juvenile marmots were not only more vigilant than were adults; they were also more responsive to the social and habitat factors that influenced vigilance behavior. As argued by Sih (1982), the degree of avoidance of predation should be proportional to the risk of predation, given a constant food regime. Since juvenile marmots are more vulnerable to predation, their greater sensitivity to factors that affect predation risk is understandable. However, as Sih pointed out, antipredator behavior should also be sensitive to the costs of predator avoidance in reduced feeding rates. Juvenile marmots are under considerable pressure to maximize food intake during their first summer of life, since survival over their first winter is directly related to their ability to gain sufficient weight to complete hibernation (Armitage et al. 1976). High predation pressure coupled with the strong need to feed efficiently consequently imposes conflicting demands upon juvenile marmots. Whereas juveniles may spend less time foraging than adults on a per minute basis, they may compensate for the lost feeding time by staying above-ground feeding later in the fall than do adults (Carey 1983).

Group size

The time that individual foraging marmots spent looking for predators decreased with increasing group size although the relationship is significant only for juveniles and yearlings (Table 1).

Vigilance behavior and group foraging in other marmot species has been described by Barash (1973) for Olympic marmots and Holmes (1979) for Alaskan hoary marmots. Both found that feeding time per minute and the frequency of look-ups per minute were less for individuals feeding near other marmots than for those foraging alone. Svendsen (1974) and Armitage (1962) found that yellow-bellied marmots living on the periphery of a colony spent more time in alert posture than those living in the colony center.

In addition to reducing the rate of food intake, looking up may also increase the conspicuousness of a marmot to its predators. My experience in trying to locate foraging marmots suggests that the animals are easier to detect when they raise their heads, and a high frequency of head movement makes them even more apparent. Thus, the decrease in vigilance with increasing group size may not only decrease the cost/benefit ratio of vigilance, but may also render individual foragers less visible to predators. However, if large groups are more noticeable to predators, the ´early warning function´ (Lazarus 1979) of group foraging may be offset, thus increasing rather than decreasing the predation risk of group members. Greater visibility of large foraging groups may therefore limit group size. Increased competition for food among group members may also limit the size of foraging groups (e.g. Silliman et al. 1977). This possibility seems unlikely for yellow-bellied marmots because feeding time and digestion rate rather than food availability are probably the limiting factors in this system (Kilgore and Armitage 1978). In the present study aggressive interactions among foraging group members were extremely rare and all colony members appeared to have free access to the foraging areas in the colony´s home range. However, because local food depletion by marmots was not measured, further testing of this hypothesis has yet to be done.

Alarm calls

The responses of marmots to alarm calls of conspecifics are variable. Some calls elicit little or no change in ongoing behaviors (such as feeding) while others cause abrupt interruption of current activity followed by quick movements to rocks for refuge or a better view of the area (Waring 1966, pers. observ.) More commonly, calls result in an increase in looking up time, supporting the hypothesis that marmots increase their antipredator activities with increases in perceived predation risk.

Habitat characteristics

The decrease in vigilance in areas of high safety burrow density suggests marmots adjusted their antipredator behavior relative to their ability to reach refuges. The influence of burrow density on vigilance behavior was much stronger for the juveniles than for the yearlings and adults (Table 1). Holmes (1979) found that young hoary marmots foraged significantly closer to a talus slope (which offered protection from predators) than did older animals. The importance of refuges to foraging area selection by marmots has been discussed by Holmes (1979) and Barash (1980), and was examined for the marmots in this study (Carey 1983).

Marmots spent more time looking up when foraging in areas of high vegetation volume than they did in more open, low volume areas. The relationship between vegetation volume and vigilance time was significant only for juveniles (Table 1), which may reflect the lesser ability of smaller animals to see over high vegetation. Jarman (1974) suggested a similar effect for small-sized antelope species relative to larger ones.

The increase in looking-up time in high volume areas is presumably due to restriction of the ability to see approaching predators as well as the visual alarm movements of other marmots. However, low food availability in these areas (Carey 1983) may have been responsible for the greater amount of time spent looking up. This hypothesis is unlikely, because a marmot foraging in an area of low food density might be expected to search for food items when it is not ingesting food. Searching for food involves moving through the vegetation with the head down, a behavior that excludes vigilance. Thus, if the need to detect predators was not necessary, marmots would spend little time looking up in high volume areas, contrary to what was observed.

Vegetation cover may also decrease the conspicuousness of a foraging marmot to its predators, thus offering protection rather than visual obstruction (Hoogland 1981, Armitage 1982). In the present study, the mean vegetation height in the areas of high vegetation volume (19 cm) was greater than the average height of an adult marmot in a head-up position (10 cm). It is therefore likely that approaching terrestrial predators (coyotes) and aerial predators coming in at a low angle (golden eagles) would be difficult for a marmot to detect in highly vegetated areas. Thus, marmots are probably more restricted, both visually and spatially, than they are protected by high vegetation.

CONCLUSIONS

Although it is not possible to measure precisely the effect of vigilance on fitness, an attempt can be made to estimate the relative impact of vigilance on marmot survival through an examination of the time and energy constraints associated with foraging in this species.

A number of studies suggest that entrance into hibernation occurs shortly after maximum body weight has been achieved (Shubin 1963, Morton et al. 1974, Morton 1975). This behavior may have considerable adaptive value, for predation risk is reduced by shortening the period of above-ground activity (Morton 1975). In addition, fall storms and low temperatures can impede weight gain by covering food with snow and increasing thermoregulatory costs, thus reducing the amount of assimilated energy that can be deposited as fat. Selection may therefore favor individuals that accumulate fat stores as rapidly as possible prior to hibernation (Morhardt and Gates 1974, Armitage et al. 1976).

Because marmots feed primarily on graminoids and forbs (Carey 1983), pursuit and handling time are for the most part inconsequential to their foraging time. If food intake is continuous, their rate of nutrient absorption is restricted largely by food quality, gut size and digestion rate, as is the case for many large herbivores (Westoby 1974). Maximum feeding efficiency to enable rapid weight gain involves filling the digestive tract, letting the food digest and the gut empty, and repeating the sequence as quickly and as frequently as possible per day. However, the need to avoid predators restricts the amount of time that can be spent ingesting food; the marmots in this study invested 10% of their foraging time in predator vigilance. This is a conservative estimate as the time and energy spent on extended look-up periods and running to burrows was not measured.

Although the feeding time lost to predator vigilance may not be critical on a daily basis, it may be significant when a seasonal strategy of energy acquisition is considered. Many factors can potentially reduce feeding time. These include unpredictable weather, high predator density, or a season of low food quantity/quality. If rapid fat accumulation and future survival are strongly related as argued above, behaviors that increase foraging efficiency without sacrificing predator avoidance would confer selective advantage by ensuring adequate preparation prior to hibernation.

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Table 1. Linear correlation coefficients between between percent of time spent looking up by foraging marmots and factors influencing looking-up time. Significant correlations are * for p $\leq$.05, ** for p $\leq$.01, *** for p $\leq$.001.

Factor	All animals (N=105)	Juveniles (N=39)	Yearlings (N=26)	Adults (N=40)
Group size	-0.331**	-0.395**	-0.571***	-0.144
Alarm calls	0.283**	0.370**	0.480**	0.054
Safety burrows	-0.252*	-0.533***	-0.161	-0.001
Vegetation volume	0.225*	0.502***	0.087	0.070
Age	-0.217*	—	—	—

Table 2. Age differences in percent of time spent looking up by yellow-bellied marmots foraging alone.

Age class	n	x±SE	F[a]	p[b]
Juveniles	13	15.8±1.2		
Yearlings	10	14.8±1.4	8.23	.001
Adults	18	9.3±1.2		

[a] ANOVA df=2,38

[b] Differences between means not significant ($p \leq .05$) for juveniles and yearlings (Duncan's multiple range test).

Table 3. Factors influencing percent of time spent looking up by foraging juvenile marmots. $R^2=.52$, $F=9.04$, $p \leq .0001$, $n=39$.

Factor	Regression coefficient	p	Contribution to R^2
Intercept	13.928	.002	
Alarm calls	5.171	.005	.128
Group size	-1.050	.053	.057
Safety burrows	-0.782	.064	.052
Vegetation volume	0.401	.161	.029

Figure 1. Percent of time ($\bar{x}$±SE) spent looking up during one-minute foraging periods by yellow-bellied marmots (all ages combined) as a function of group size. Sample sizes are shown in parentheses. N=105.

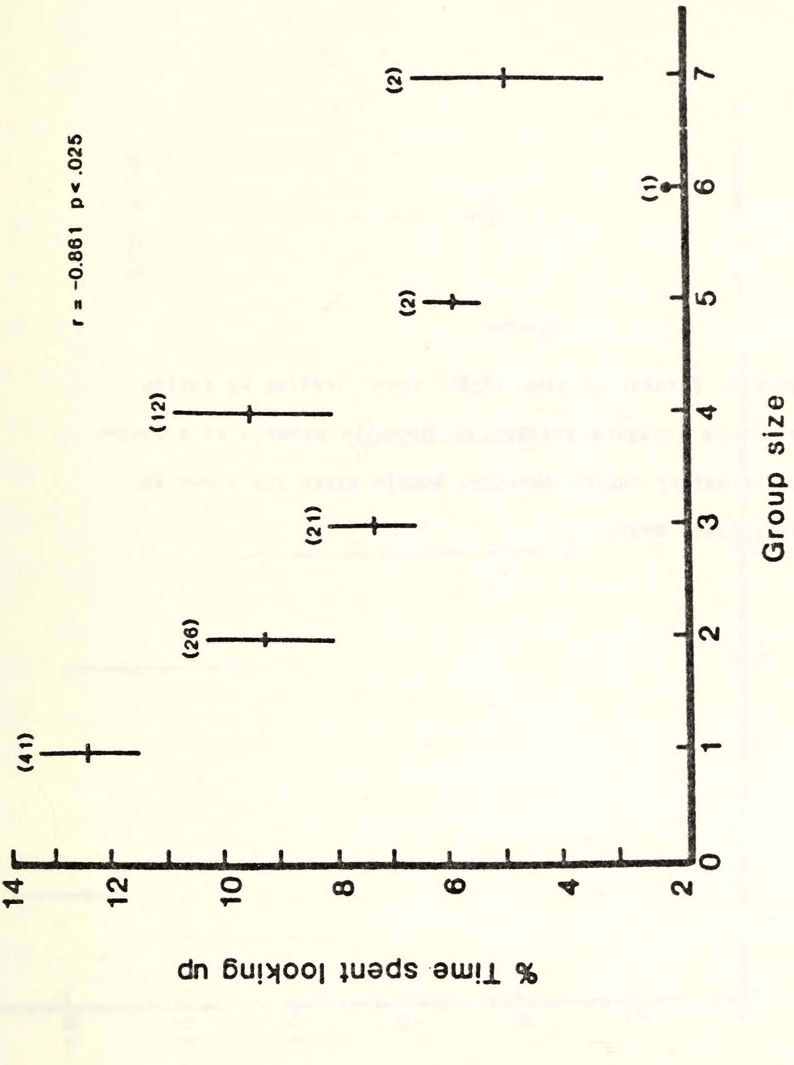
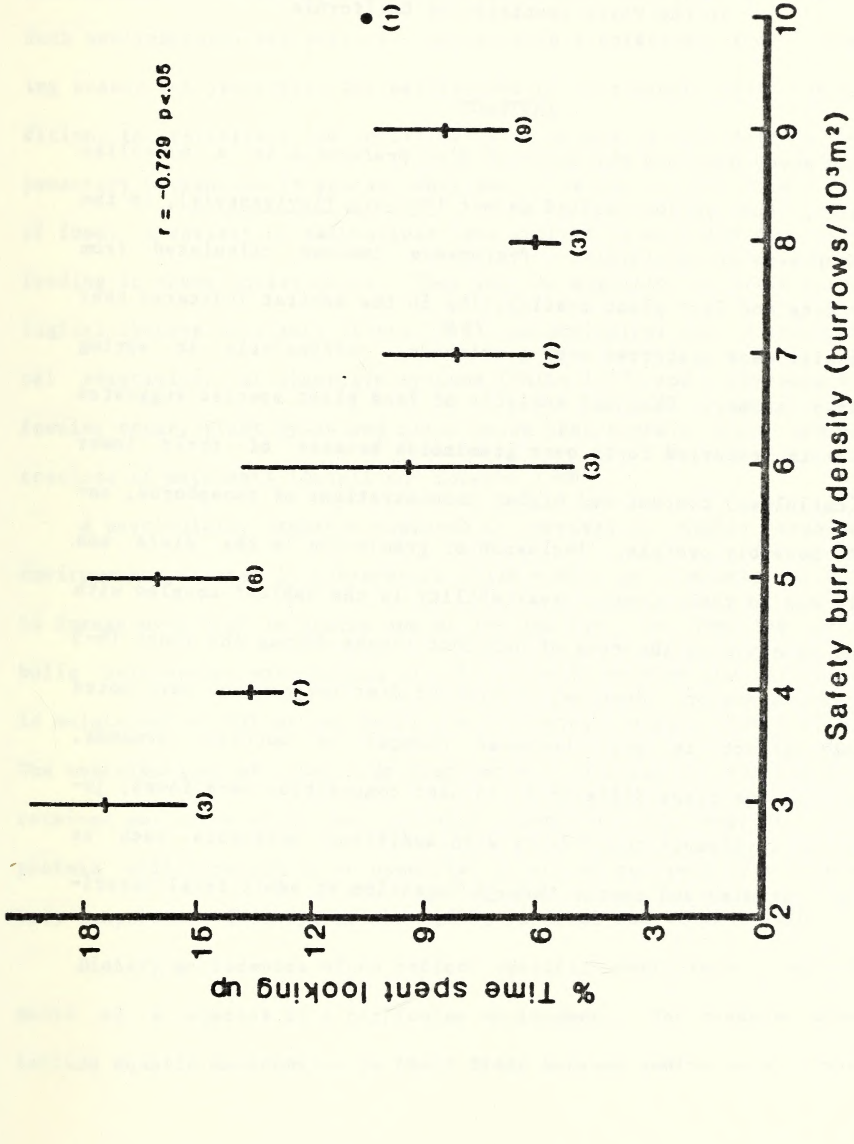

r = -0.861 p < .025
% Time spent looking up
14
12
10
8
6
4
2
Group size
0
1
2
3
4
5
6
7
(41)
(26)
(21)
(12)
(2)
(1)
(2)

Figure 2. Percent of time ($\bar{X}\pm$SE) spent looking up during one-minute foraging periods by juvenile marmots as a function of safety burrow density. Sample sizes are shown in parentheses. N=39.


r = −0.729 p<.05
% Time spent looking up
0
3
6
9
12
15
18
Safety burrow density (burrows/10³m²)
2
3
4
5
6
7
8
9
10
(3)
(7)
(6)
(3)
(7)
(3)
(9)
(1)

CHAPTER 2

The Nutritional Ecology of Yellow-bellied Marmots in the White Mountains of California

ABSTRACT

This study examined the basis of diet preference in a mammalian hibernator, the yellow-bellied marmot (Marmota flaviventris), in the White Mountains of California. Preference indexes calculated from dietary data and food plant availability in the habitat indicated that forb species were preferred over graminoids, particularly in spring and early summer. Chemical analysis of food plant species suggested that marmots preferred forbs over graminoids because of their lower fiber (cellulose) content and higher concentrations of phosphorus, sodium and possibly protein. Inclusion of graminoids in the diets was probably due to their greater availability in the habitat coupled with the need to maximize the rate of nutrient intake during the short (4-5 month) active season. Seasonal changes in diet composition were noted which may reflect in part temporal changes in nutrient demands. Although no age class differences in diet composition were found, juveniles may supplement their diets with additional nutrients such as protein, vitamins and energy through ingestion of adult fecal material.

INTRODUCTION

Strong seasonal fluctuations in food quality and availability characterize the feeding regime of many arctic and alpine herbivores. Such environmental periodicity, coupled with a relatively short growing season can jeopardize the maintenance of an adequate diet. In addition, the relatively low nutritive value of most plants demands compensatory mechanisms to extract what nutrients are present from a bulk of food. A variety of adaptations have evolved to meet the demands of feeding in these environments. They include migration to track phenological changes in plants (Klein 1968), morphological and physiological adaptations of digestive systems (White 1975) and preference for feeding areas, plant types and plant parts that contain high concentrations of nutrients (Batzli and Sobaski 1980).

A particularly dramatic approach to survival in highly seasonal environments is seen in hibernators which reduce or eliminate the need to forage when food is scarce and of low quality. By lowering metabolic rate energy expenditure is substantially reduced and the animal is maintained on fat stores until the next active season (Young 1976). The contributions of other body components to hibernation success have received much less attention, although recent evidence suggests that protein utitilization is an essential aspect of survival at a lowered body temperature (Montoya et al. 1978, Riedesel and Steffen 1980).

Dietary preferences often reflect specific nutritional requirements of a species in a particular environment. For example, moose include aquatic macrophytes in their diets because sodium is a limiting mineral for them (Belovsky 1978). Arctic caribou and reindeer maintain winter diets high in lichens to provide a readily fermentable supply of carbohydrate for microbial synthesis of protein (White 1975). Forage selection patterns may also be the result of avoidance of plant secondary compounds that are detrimental to herbivore fitness (Bryant and Kuropat 1980).

The present study was designed to determine if a hibernating mammal chooses a diet based on food availability or if plants are selected for their nutrient contents. The hibernator studied was the yellow-bellied marmot (Marmota flaviventris), a medium-sized (2-4 kg) nonruminant herbivore distributed in mountainous areas of western North America (Frase and Hoffmann 1980). To the investigate the basis of diet selection in this species I considered two potential influences on diet composition. First, because food availability and the nutritional demands of a hibernator may vary over the active season I determined diet composition and food abundance periodically as the season progressed. The effect of age on food preference was also considered because the degree to which a diet fulfills the nutrient requirements of a species may not be the same for all members of a population (Clark 1980). For example, the requirements of young, growing animals and reproductive females are generally more stringent than for other age classes, particularly in regard to protein and minerals (Robbins 1983). In addition, the consequences of inadequate food intake may vary with age; overwinter mortality is highest among juvenile marmots and is inversely related to prehibernation weight (Armitage et al. 1976).

The results of the study revealed that marmots select plant types that are easily digested and high in certain essential nutrients. Although no age differences in diet composition were found, seasonal changes in diet occurred which may in part reflect temporal changes in nutrient demands.

MATERIALS AND METHODS

Study area

The study was conducted in MacAfee Meadow (37 35´N, 118 12´W) at 3650 m in the White Mountains of California during the spring and summer of 1982. The site is dominated by graminoids (grasses and grass-like herbs, principally Carex spp., Juncus spp., Deschampsia caespitosa) in moist areas on the meadow floor and alpine steppe species (Koeleria cristata, Trifolium monoense) in drier, elevated portions of the meadow and on the surrounding slopes. Data were collected from 25 marmots (8 juveniles, 8 yearlings, 9 adult females) whose collective feeding range was approximately 2 hectares. At least six of the adult females gave birth in the spring. Because adult males were rarely seen in the study area after the breeding season no dietary information was collected on this age class.

Diet analysis

Microhistological analysis of plant fragments in fecal material was used to estimate the percentage composition of plant taxa in the marmots´ diets. Fecal samples were collected from live-trapped marmots during each of three time periods: spring (6-28 May), early summer (2-28 June) and midsummer (2 July through 9 August). The spring period spans the time between adult emergence from hibernation and the approximate time of parturition. Spring samples were only from adult females. The early summer period extends from parturition until first emergence of juveniles above-ground from their natal burrows and includes samples from adult females and yearlings; the mid-summer period, which includes samples from all 3 age classes, began at the time of juvenile appearance and continued until trapping success decreased. Samples from the same individual were collected on different days. A total of 68 samples was analyzed.

Fecal pellets were oven-dried the same day of collection and later ground over a 20-mesh screen to produce fragments of uniform size. The ground material was then washed in a mild detergent solution, rinsed and soaked in bleach for 1 h to remove pigments. After a final rinse, the material was suspended in alcohol and mounted on microscope slides with glycerin jelly. Care was taken to transfer the same amount of material to each slide in order to obtain an average of 3 identifiable fragments per microscope field when viewed at 100X. The 'frequency addition' procedure, recommended by Holechek and Gross (1982), was used to estimate the dry weight composition of each sample. This procedure involves determining the frequency of occurrence of each plant species in 100 microscope fields and dividing the frequency of each species by the total number of frequencies for all species.

Attempts were made to classify plant fragments to species using reference slides prepared from tissues of plants collected in the study area. While some fragments were recognizable as particular species, most could only be categorized as either monocotyledons or dicotyledons ('graminoids' or 'forbs'). The data were summarized as mean dry weight percentages for the 2 plant types. Diet composition was also determined qualitatively by direct observation of marmots feeding on specific plants and by inspection of plants for evidence of consumption after an animal had fed in an area.

To account for differential digestibility of plant species, correction factors were obtained through feeding trials with captive marmots according to the procedure outlined in Brand (1978). Two forb species (Trifolium monoense and Haplopappus apargioides) and one grass (Koeleria cristata) were used in the trials. These species were determined to be major dietary components by frequency in the fecal samples, direct field observation and laboratory preference tests. Relative coefficients of digestiblity were close to 1.0 for all 3 species, thus the 'frequency addition' procedure was assumed to give a 1:1 relationship between % composition of plant types in the samples and relative dry weight of plants in the diet.

Vegetation analysis

Food availability in the colony's feeding range was estimated during early summer and midsummer by sampling vegetation along 11 50-meter transects. Ten placements of a 1 m^2 quadrat from which 10 points were sampled resulted in a total of 100 points per transect; 1100 points were thus sampled in the entire study area and converted to percentage of total plant cover for each species. Biomass estimates were obtained by clipping above-ground vegetation within 1 dm^2 of each species and drying at 100° C to a constant weight. This value was multiplied by the percentage cover estimates to obtain dry weight biomass in g/m^2 for each plant type.

A preference index (PI) was calculated for each plant type in the diet such that PI = mean percentage dry weight of a plant type in the fecal samples divided by the relative abundance (dry weight biomass) of the plant type in the habitat. Only those species used for food by the marmots were included in the total availability measures because not all species of a given plant type were eaten. A PI = 1.0 indicates intake proportional to abundance in the environment and a PI > 1.0 indicates selective preference for a plant type.

To determine if marmots were choosing plants on the basis of their nutritional quality, plant samples were collected from the study area during midsummer for chemical analysis. Samples were dried at 60° C and analyzed for percentage dry matter composition of sodium, calcium, phospohorus and total Kjeldhal nitrogen (nitrogen values were later converted to % protein by multiplying by 6.25). Cellulose and lignin, two indicators of plant ´fiber´ (Van Soest 1982), were also measured. Cellulose is a polysaccharide constituent of plant cell walls that cannot be degraded by vertebrate digestion but can be broken down through fermentation by bacterial enzymes (Gibson 1968). Lignin is a high molecular weight, nonsaccharide polymer that adds rigidity to cell walls. It is resistant to normal hydrolysis and fermentation, and is therefore indigestible.

RESULTS

Diet composition

The mean percentage occurrence of forbs and graminoids in the diets are presented in Table 1. The most commonly occurring identifiable plant fragment was the legume, Trifolium monoense; its relative abundance in the diets was 8% in spring, 45% in early summer and 56% in midsummer.

The proportion of forbs in all fecal samples increased significantly from spring to midsummer (Table 1). This may have been due in part to the increase in abundance of preferred forbs in the feeding range of the colony during this time (Table 2, spring vegetation was not sampled). Nevertheless, the preference indexes (Table 3) show that the increase in the forb fraction of diets was a reflection of actual preference for this plant type over graminoids. Graminoids were more abundant than forbs during both summer periods, yet forbs dominated the diets. The forb : graminoid ratio in the diets was 25 times that of the same ratio in the habitat in early summer, and almost 4 times greater in midsummer.

Age variations in diet composition may also have caused the temporal differences observed. To investigate this possibility, samples from the 2 summer periods were analyzed by age class. There were no differences in the proportion of plant types in the fecal samples between yearlings and adults in early summer ($t=1.17$, $P>.10$), or between all three age groups in midsummer (Table 4).

Nutritional quality of the diet

Chemical constituents of forb and graminoid species identified as food items through observation and/or fecal analysis are compared in Table 5. Of the two fiber components, only cellulose content differed between the 2 plant types, being lower in the forbs. Forbs also contained higher concentrations of phosphorus and sodium. Calcium and protein content were not significantly different between the forbs and graminoids tested.

DISCUSSION

The preference for forbs over graminoids exibited by these marmots could be related to the differences in fiber content of the two plant types. The nutritive value of the plant cell wall is a function of its digestibility; digestibility varies with cell wall composition and the digestive system of the animal (Robbins 1983). In general, both voluntary intake and digestibility are negatively correlated with fiber content (Van Soest 1982). Because the extent of fermentation of fibrous foods varies inversely with passage rate through the gut and passage rate varies directly with body size, small nonruminant herbivores should select foods of high nutritive value which can have much faster fermentation rates (Parra 1974).

These arguments suggest that a forb diet, being low in fiber, would be more digestible by marmots than one composed of graminoids. Although marmots clearly preferred forbs to graminoids, graminoids always made up at least 25 % of the diets analyzed throughout the study. The inclusion of graminoids in the diets may have been due to the relative abundance of the 2 plant types in the environment coupled with constraints on food ingestion apart from food quality. A high rate of food intake may be very beneficial to marmots because factors such as thermoregulatory stress (Belovsky 1981) and predator avoidance (Carey 1983) can reduce foraging time. Graminoids are relatively bulky and easily obtained; they therefore fill the gut in less time than required for forbs. Although the ability of marmots to ferment fibrous foods has not been investigated, a number of other rodents can produce volatile fatty acids (fermentation products) in the cecum (Johnson and McBee 1967, McBee 1970, Hoover and Clarke 1972). Marmots may therefore be able to utilize cell wall material to some extent. Thus, the selection of a mixed diet composed of readily available but lower quality graminoids and less available, highly digestible forbs may represent a balance between intake of easily digestible food items and maximization of food intake rate.

The marmots appeared to show preferences for specific nutrients, a behavior which has been reported for a variety of species. Protein is probably the most critical and often limiting nutrient (Bell 1971, White 1978, Milton 1979). Although the protein content of forbs did not differ significantly from that of graminoids, the predominance of the legume Trifolium monoense in marmot diets may have been due to the high protein levels characteristic of this plant family (Graham 1940). Trifolium monoense is the most common non-graminoid species in diets of White Mountain bighorn sheep (Wehausen 1983). Hansen (1975) found that hoary marmots in Alaska did not ingest plants in proportion to their availability but rather preferred certain plants over others, particularly 2 species of legumes.

The preference for forbs may also be related to selection of plants high in phosphorus content; forbs were significantly higher in phosphorus than were graminoids. This mineral, which is involved in almost every aspect of animal metabolism and especially bone growth (Robbins 1983) may be a limiting nutrient for herbivores (Ozanne and Howes 1971, Wehausen 1983). High protein and phosphorus content were associated with foods chosen by the northern hare, Lepus timidus (Lindlof et al. 1974), Sierra Nevada bighorn sheep, Ovis canadensis (Wehausen 1980) and caribou Rangifer tarandus (Klein 1968).

Calcium, another mineral critical for the growth of skeletal material, did not differ significantly between the forbs and graminoids analyzed. Although correlation of food preference order and calcium content has been reported in other species (e.g., Lindlöf et al. 1978), no relationship between calcium and food preferences of marmots was revealed by the present study. However, the calcium contents of the 2 principal forb species eaten by the marmots (Trifolium monoense, 1.325 % and Haplopappus apargioides, 1.227 %) were 2-3 times higher than that of any other plant species analyzed.

Sodium appears to be a limiting nutrient for many animals, particularly in seasons and environments in which sodium is deficient (Aumann and Emlen 1965, Blair-West et al. 1968, Weeks and Kirkpatrick 1976). Weeks and Kirkpatrick (1978) demonstrated that woodchucks (Marmota monax) have a strong preference for sodium, particularly in the spring. In the present study, the high preference index for forbs in spring and early summer may be related to nutrient depletion from hibernation and increased sodium demand by lactating females (Robbins 1983). I observed marmots licking soil soon after spring emergence, a behavior that has been attributed to sodium deficiency in woodchucks and other species (Hebert and Cowan 1971, Weir 1972, Weeks and Kirkpatrick 1978).

Seasonal changes in nutrient quality of plants are known to influence dietary choices of a variety of species (Moss 1972, Glander 1981). New growth and reproductive structures (flowers, seeds) generally contain more protein, less fiber and lower levels of secondary compounds than do mature leaves and stems (Feeny 1970, Milton 1979). New shoots and rhizomes of grasses and sedges, and roots of _Trifolium monoense_ were ingested by the marmots, particularly during the first few weeks after emergence from hibernation. These plant parts are generally higher in calories and nutrients than the entire plant due to reserves stored from the prior season productivity (Bliss 1962). Difficulty in separating flower parts from other plant material precluded quantitative measurement of their proportions in the diets. However, ingestion of flowers and seed heads of certain forbs and graminoids was commonly observed.

No age-related differences in diet composition were found for the marmots in this study although the use of foraging areas did vary between juveniles, yearlings and adult females (Carey 1983). Nevertheless, the hypothesis that juveniles may exhibit different dietary preferences as a consequence of their greater nutrient demands is supported by 6 observations of coprophagy by juveniles recorded over 3 summers. Although the ingestion of feces by lagomorphs and a number of rodent species has been known for some time (Kenagy and Hoyt 1980), it has not previously been reported in the genus _Marmota_. In the present study, yearlings and adults were never observed ingesting feces, and it appeared that the juveniles were ingesting adult fecal pellets rather than their own. Although the actual benefit of this behavior to juvenile marmots is as yet unclear, coprophagy may provide additional quantities of a variety of nutrients including protein (Robbins 1983) and B-vitamins (Hörnicke and Björnhag 1980). Although ingestion of fecal material competes with food for animals with an abundant food supply, when food is limited or has a very low digestiblity ingestion of feces can increase energy intake to some extent (Hörnicke and Björnhag 1980). Juveniles may therefore benefit from fecal ingestion simply by gaining more energy than they would on a plant diet alone.

CONCLUSIONS

The results of this study indicate that marmots prefer plants that are low in fiber and high in essential nutrients, particularly phosphorus, sodium and possibly protein. These results agree with recent theoretical and empirical work which suggests that intake of a variety of nutrients within a given bulk of food may be the primary objective of a foraging animal (Pulliam 1975, Clark 1980), particularly for herbivores (Westoby 1974, Milton 1979). Nonetheless, the composition of the marmot diet is probably related to a number of factors including plant nutrient content, food plant availability, time available for feeding, and the nutritional requirements of a marmot at any point in its annual cycle.

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Table 1. Composition of marmot diets estimated from fecal samples collected 6 May through 9 August 1982. See text for description of time periods. Shown are means (± SE).

	Frequency of occurrence in diet			
Plant type	Spring (N=13)	Early summer (N=18)	Midsummer (N=37)	P[a]
Forbs	0.225 ± 0.057	0.602 ± 0.027	0.718 ± 0.029	<.001
Graminoids	0.775 ± 0.057	0.398 ± 0.027	0.282 ± 0.029	

[a] F=42.6, df=2,66; all dietary proportions are significantly different from each other as determined by Newman-Keuls multiple range test

Table 2. Food plant abundance in the feeding range of marmots in early summer and midsummer. Shown are means (± SE).

	Early summer		Midsummer	
Plant type	Biomass g/m^2	% of total	Biomass g/m^2	% of total
Forbs	3.2 ± 1.2	.06	40.0 ± 8.2	.40
Graminoids	49.9 ± 25.4	.94	60.6 ± 11.1	.60

Table 3. Preference indexes and forb : graminoid ratios in diets of yellow-bellied marmots. See text for description of time periods.

Preference index[a]	Early summer (N=18)	Mid summer (N=37)
Forbs	10.05	1.80
Graminoids	0.42	0.47
Forb : graminoid		
Diet	1.51	2.58
Feeding range	0.06	0.66
Diet : feeding range	25.20	3.91

[a] Preference index = % occurrence in diet : % abundance in feeding range of colony, calculated from data presented in tables 1 and 2.

Table 4. Composition of marmot diets by age class. Values are mean (± SE) percentage occurrence in fecal samples collected during mid-summer (2 July -9 August 1982).

Plant type	Juveniles (N=16)	Yearlings (N=11)	Adults (N=10)	P[a]
Forbs	0.700 ± 0.058	0.762 ± 0.036	0.699 ± 0.035	NS
Graminoids	0.300 ± 0.058	0.238 ± 0.036	0.301 ± 0.035	NS

[a] ANOVA for age class dietary proportions F=0.48, df=2,34; P>.50

Table 5. Chemical composition of forbs and graminoids in marmot diets during midsummer. Shown are mean (± SE) values for species analyzed.

Nutrient[a]	Forbs[b]	Graminoids[c]	P[d]
Cellulose	15.26 ± 1.84	25.38 ± 0.67	<.01
Lignin	5.11 ± 0.64	3.47 ± 0.41	>.05
Protein	17.58 ± 2.11	12.40 ± 1.86	>.10
Phosphorus	0.313 ± 0.058	0.145 ± 0.017	<.05
Calcium	1.059 ± 0.169	0.402 ± 0.039	>.05
Sodium	0.017 ± 0.003	0.006 ± 0.001	=.052

[a] Percentage of dry matter; % protein = % nitrogen x 6.25.

[b] Forbs analyzed are leaves and stems of *Trifolium monoense*, *Haplopappus apargioides*, *Rumex paucifolius*, *Lewisia pygmaea*, *Potentilla pseudoscericea*.

[c] Graminoids analyzed are leaves and stems of *Koeleria cristata*, *Carex eleocharis*, *Juncus mexicanus*, *Festuca brachyphylla*.

[d] Mann-Whitney test.

CHAPTER 3

The Use of Foraging Areas by Yellow-bellied Marmots

ABSTRACT

This study examines the use of foraging areas by a colony of yellow-bellied marmots (Marmota flaviventris) in the White Mountains of California. Usage indexes that represent the amount of time 26 marmots fed in each of 11 foraging areas were obtained through scan-sampling of the colony's movements and correlated with habitat variables using univariate and multivariate techniques. Marmots preferred to forage in certain areas over others; of the 11 areas, 5 were preferred (used more often than expected based on relative size), 3 were less preferred and the remainder were used in proportion to their availability. Preference for foraging areas was positively correlated with food plant biomass and negatively correlated with dense, high vegetation. I interpret these results as adaptive behavior integrating the simultaneous demands of food ingestion and predator avoidance. Age-class similarity in foraging patterns was greatest between yearlings and adults and least between juveniles and yearlings. The behavior of juveniles reflected most clearly the relationships between foraging area preferences and habitat characteristics, whereas yearlings appeared to use foraging areas largely in response to variables not measured in the study. Age-specific variations in foraging patterns may reflect the risks associated with predation and inadequate nutrition, which vary with age.

INTRODUCTION

Although the movements of a foraging animal should be related to the distribution of food resources (Royama 1970, Schoener 1971), numerous studies have indicated that other considerations besides food can influence where an animal chooses to feed (e.g., Barash 1980, Belovsky 1981, Duncan 1983). For instance, the need to avoid predators can have a strong influence on foraging patterns (Stein and Magnuson 1976, Sih 1982, Cerri and Fraser 1983). Habitat characteristics that simultaneously facilitate food acquisition and predator avoidance may not always occur in the same location. Thus, animals must often respond to a variety of indicators of habitat quality in their choice of feeding areas.

The reasons why animals choose to feed in certain areas over others may also vary among individuals within a population. Stein and Magnuson (1976) and Sih (1982) provide evidence that the degree to which predators modify foraging behavior is related to the magnitude of the risk of predation. In both studies, the most susceptible age class (juveniles) exhibited the greatest degree of adjustment in foraging movements in response to the presence of predators.

This study of foraging area use by yellow-bellied marmots (Marmota flaviventris) demonstrates age-specific variations in foraging patterns. Differences in the use of foraging areas is shown to be related not only to the risk of predator attack but also to the risks associated with inadequate nutrient intake. I first show that marmots prefer certain foraging areas over others and outline the habitat characteristics associated with these preferences. I then demonstrate that the relative use of foraging areas differs among 3 age classes of marmots and discuss the risk-sensitive basis of age-specific foraging patterns.

METHODS

Study animal

Yellow-bellied marmots (Rodentia: Sciuridae) are hibernating rodents inhabiting mountainous and high latitude regions in western North America (Frase and Hoffmann 1980). In the White Mountains, site of the present study, adult marmots emerge from hibernation in late April and mate soon afterwards. Yearlings (animals in their second summer) emerge in late May and do not reproduce until the following year as adults. Juveniles are born after a 30-day gestation period (Frase and Hoffmann 1980) and first appear aboveground during the first week of July at the time of weaning. Adults cease aboveground activity by early September; yearlings and juveniles are absent from the study area by mid September.

Deposition of sufficient body fat during the active season is critical for maintenance during the subsequent hibernation period. Overwinter mortality is highest for juveniles and is inversely related to prehibernation weight (Armitage et al. 1976). Marmots are preyed upon by a variety of aerial and terrestrial predators, including coyotes (Canis latrans) and golden eagles (Aquila chrysaetos). Antipredator behavior of marmot species has been shown to vary with age, foraging group size, and structural characteristics of foraging areas that may affect the ability to detect and escape from predators

(Barash 1973, Holmes 1979, Carey 1983).

Study area and measurement of habitat characteristics

I studied the feeding ecology of yellow-bellied marmots in MacAfee Meadow (37 35′N, 118 12′W) at 3650 meters elevation in the White Mountains of eastern California during the summers of 1980-1982. The data presented here are based on 172 hours of observation of one colony of yellow-bellied marmots during the summer of 1982. ′Colony′ refers to marmots that had full and exclusive use of feeding areas surrounding a common home sleeping site. All marmots in the colony used the same foraging areas; non-members were usually chased off by colony residents. The sleeping burrows of the marmots were located around a rock outcrop on the floor of the meadow. The meadow is dominated by graminoids (grasses and grass-like herbs, principally Carex spp., Juncus spp., Deschampsia caespitosa) and some forbs common to moist areas (e.g., Gentiana newberryi, Ivesia lycopodioides). Total vegetation cover in this region is high (over 90%) due to the density of graminoids. The surrounding slopes are largely dry sites characterized by a higher diversity of plants than is the meadow floor and contain more species of forbs. Vegetation cover in dry areas averages 60%. Although the physiognomic distinction between the meadow floor and the slopes is apparent, dry areas are found as elevated portions of the meadow floor and moist areas also occur higher up on the slopes in drainage zones.

The total feeding range of the colony (2 ha) was divided into 11 foraging areas based on physiognomy and distance from the sleeping burrows. Eleven habitat characteristics (Table 1) were measured in each area during two time periods: midsummer (7 July to 15 August) and late summer (16 August to 9 September). Percent cover of plant species was determined by a combined point quadrat-linear transect technique using methods outlined in Mueller-Dombois and Ellenberg (1974). For each species above-ground vegetation within 1 dm^2 was clipped and dried at 100°C to constant weight. The resulting value was multiplied by the percent cover of the species in each area to estimate species biomass. Food plants were identified through field and laboratory observations and microhistological analysis of fecal samples (Carey 1983). These methods identified Trifolium monoense (Leguminosae), Haplopappus apargiodes (Compositae) and Koeleria cristata (Gramineae) as major dietary items. Biomass estimates of 8 plant species eaten by the marmots were combined as total food biomass.

Vegetation volume was calculated by measuring the mean height of all plants that extended 5 cm or higher above the ground surface and multiplying this value by the plant cover. Most of the species that met the height criterion were not used as food by the marmots. Safety burrows are excavations made by marmots in feeding areas. The measurement of safety burrow density also included sleeping burrows, since marmots sometimes fed near the home site. The size of each foraging area and the distance of each area's center to the general vicinity of the sleeping burrows were also recorded.

Colony composition and observations of foraging area use

In 1982 the colony was composed of 26 individuals: 15 juveniles, 5 yearlings, and 6 adults. All 6 adults were females that had given birth in the spring of 1982; no adult males were resident in the colony during the study. Marmots were ear tagged and marked for visual identification with fur dye (Nyanzol D). Observations were made from a tower (5.5 m) at one edge of the colony's home range. The behavior and location of each colony member were recorded at 15 minute intervals during the peak foraging times (0600-1000 h, 1500-1900 h) using a scan-sampling technique (Altmann 1974). Marmots could easily traverse the entire colony range within 15 min; the observations were therefore assumed to be independent. Relative use of the 11 foraging areas during each time period was determined by calulating a usage index that represented the proportion of total sightings of marmots feeding in an area out of the total number of sightings in all areas. Each foraging area was assigned a usage index and the 11 areas were ranked in increasing order of use. This procedure was carried out for all ages combined and for each age class separately.

Because of intercorrelations among habitat variables as well as the possibility that marmots were responding to combinations of variables rather than to a number of variables independently, the habitat data were subjected to a factor analysis (BMDP4M, Dixon 1981). This multivariate technique reduces the number of original variables to a smaller set of uncorrelated composite variables, or factors, that account for the underlying variation among the data. Those factors with eigenvalues >1.0 were retained and subjected to orthogonal varimax rotation to improve factor loadings (Cooley and Lohnes 1971, Harris 1975). Only 10 of the 11 habitat variables were used in the factor analysis due to restrictions on the number of variables that could be entered. Distance to sleeping burrows was the variable chosen to omit because of its lack of correlation with usage indexes (see results, Table 3). Foraging areas were ranked on the basis of their factor scores and Spearman rank correlations were performed on the ranks derived from the usage indexes and those from factor scores to examine the relationships between factors and patterns of area use. The generality of the factor analysis in explaining foraging patterns was tested by using the factor models derived from midsummer data to predict usage patterns in late summer when some of the habitat variables had changed (Table 1). New factor scores were calculated for each foraging area using the following equation:

$$FS_h = \sum_{i=1}^{10} FSC_i \; (X_{ih} - \bar{X}_i \; / \; SD_i),$$

where FS_h = factor score for area h in late summer; FSC_i = factor score coefficient for habitat variable i in mid summer (from the factor algorithm derived from the midsummer data); X_{ih} = value of variable i in area h in late summer; $\bar{X}_i$ = mean of variable i over all areas in late summer; SD_i = standard deviation of variable i in late summer. Areas were again ranked as outlined above and correlated with usage indexes calculated from late summer observations of foraging area use.

In addition, rank correlations were performed between individual habitat variables and usage indexes to further explore relationships between habitat characteristics and patterns of area use.

RESULTS

Use of foraging areas

Marmots preferred certain foraging areas to others (Table 2). Chi square analysis on numbers of animals observed in foraging areas compared to expected values based on area size was significant (x^2 =1053.0, $P \leq 0.0001$, all ages combined). Examination of each area's contribution to the x^2 (+ signifies greater than expected and - signifies less than expected) indicated that 5 areas were 'preferred' (contrib. to $x^2 \geq 9.0+$), 3 areas were 'less preferred' (contrib. to $x^2 \leq 9.0-$) and the remainder were 'neutral' ($0.0 < x^2 \leq 0.7+$).

Foraging area preferences of each age class are shown in Table 2. Similarity between age classes in foraging patterns was evaluated by Spearman rank correlation analysis on usage indexes calculated for each class. Adults and yearlings overlapped considerably in their use of foraging areas (r =0.822, $P \leq 0.02$), as did juveniles and adults (r =0.745, $P \leq 0.05$). Yearlings and juveniles were least similar in their foraging patterns (r =0.534, $P > 0.05$).

Multivariate factors influencing use of foraging areas

Two factors were extracted by the analysis which together account for 83.2% of the variability in the habitat data (Table 4). Biologically meaningful descriptions of factors can be obtained from factor loadings which express the correlation of an original variable with a factor that has been extracted. A factor can therefore be named by those variables having the highest loadings in absolute value on the factor. Factor one, which accounts for 66.3% of the variance in the data represents a gradient from dry, sparsely vegetated areas containing high food biomass (high factor scores) to moist areas with high total vegetation cover dominated by tall, non-food plants (low factor scores). Factor 2 accounts for an additional 17% of the variability in the data; high scores on this factor represent high abundance of Haplopappus and high safety burrow density. Vegetation volume and height also load moderately (negative) on this factor, although they are more strongly correlated with factor 1.

Foraging area use in midsummer has a significant positive relationship with the habitat dimension represented by factor 1 (Table 5). Thus, marmots appeared to spend more time foraging in areas containing high food plant abundance and low vegetation height and cover. The lack of correlation between area use and the habitat variables represented by factor 2 suggests that marmots did not choose foraging areas on the basis of safety burrow density or Haplopappus biomass. The relationship between area use and factor 1 was strongest for the juveniles and weakest for the yearlings (Table 5).

The correlations between usage indexes and factor 1 scores derived from late summer data (Table 5) are not as strong as those that resulted from the midsummer analysis, but they are significant ($P \leq 0.05$) for all age groups other than yearlings. There were no significant correlations between area use and factor 2 scores in late summer.

Individual variables influencing use of foraging areas

Overall, the univariate correlations confirm the results of the factor analysis; the use of foraging areas was positively correlated with food plant biomass and negatively correlated with soil moisture and dense, high vegetation (Table 3). In addition, they offer more insight into some of the individual relationships between variables than were revealed through the multivariate analysis and help localize the age class differences in foraging patterns.

The abundances of Koeleria cristata and Trifolium monoense were associated with area use although only juveniles appeared to be choosing foraging areas on the basis of Trifolium biomass (Table 3). The abundance of Haplopappus apargioides, another species eaten by the marmots, was not related to foraging patterns of any age group. In contrast to Trifolium and Koeleria, Haplopappus occurs both in moist and in dry sites although its distribution is sporadic in more mesic, highly vegetated areas. The negative correlation between usage indexes and total vegetation cover may therefore have obscured any influence Haplopappus biomass might exert on usage patterns. Indeed, when the same analysis is performed using only the 6 areas of lowest total vegetation cover, Haplopappus biomass is significantly related to area use ($r=0.883$, $P\leq0.02$).

An inverse relationship between food plant abundance and total vegetation cover ($r=-0.801$, $P\leq0.01$) made it difficult to separate their independent effects on foraging area use (c.f. Thompson 1982). Correlations were therefore run using only the 6 areas of highest food biomass (> 77 g/m^2). When this was done, area use was still negatively correlated with vegetation cover ($r=-0.943$, $P\leq0.005$), and positively correlated with food biomass ($r=0.886$, $P\leq0.02$) which supports the hypothesis that area use is influenced by vegetation structure even when food is relatively abundant.

In agreement with the mutivariate results, the number of significant correlations between habitat characteristics and usage indexes was greatest for juveniles (8) and least for yearlings (2).

DISCUSSION

Marmots were responsive to habitat characteristics that affected their ability to obtain nutrients (high food plant biomass) and detect predators (low vegetation height and cover). This result suggests that marmots showed adaptive behavior integrating the simultaneous demands of food ingestion and predator avoidance (Holmes 1979, Sih 1980b). Feeding in areas with low vegetation may enhance predator detection by increasing visual range over that in areas with taller vegetation, although there may be some trade-off between concealment for the prey and the predator (Armitage 1982, Carey 1983). In addition, marmots feed at higher rates in areas containing low vegetation because the amount of time spent scanning for predators is reduced in areas with low vegetation volume (Carey 1983). The possibility that marmots preferred to forage in areas with low vegetation solely because of high food biomass in these areas cannot be entirely ruled out based on the data presented here. Nonetheless, the strong negative correlation between area use and vegetation height in areas with abundant food suggests that the ability to detect approaching predators does indeed influence foraging area preference. Evidence from other species suggests that food density may be the most important determinant of foraging area use (Holmes 1979, Cerri and Fraser 1983, Duncan 1983) followed by structural variables such as vegetation height and distance to refuges (Holmes 1979, Fraser and Sise 1980, Burger 1982, Thompson 1982).

Given that marmots spent less time scanning for predators (and more time eating) when foraging in areas of high safety burrow density (Carey 1983) it is surprising that the effect of burrow density on area use was neglible. Holmes (1979) found that foraging patch use by hoary marmots (Marmota caligata) was best explained by a linear combination of forage and risk factors, i.e., frequency of selected plants (the forage factor) and the number of refuge burrows in a patch and the patch's distance from the talus (the two risk-factor variables); his analysis did not include total vegetation cover and height. However, the lack of correlation between area use and safety burrow density in the present study may be explained by numerous observations of marmots running up onto rocks or to higher ground rather than into a burrow upon hearing an alarm call. These observations suggest that the distance at which a predator is detected may be more important to a foraging marmot than the distance to the nearest refuge.

Age class differences in foraging patterns

The pattern of foraging area use by yearlings was distinct from that of juveniles and adults, both in proportionate use of areas and in its lack of association with most of the habitat characteristics that were highly correlated with juvenile and adult usage patterns. In contrast, juvenile behavior showed most clearly the direction and magnitude of the relationships found in the study. Differential sensitivity to variations in predator avoidance and food intake may be responsible for age class differences in foraging patterns.

Several studies have suggested that the most dramatic behavioral adjustments in response to predation risk occur among individuals most vulnerable to predation. Sih (1982) showed that early instar juvenile backswimmers (Notonecta hoffmanni) which are most susceptible to predation utilized the most costly means of avoidance, i.e, reduction of movement and a shift in patch use. These alterations resulted in a 30-50% reduction in their feeding rate. Similarly, Stein and Magnuson (1976) found that the response of different age, sex and size groups of crayfish to predators is related to their susceptibility. As vulnerability to predation rises, crayfish behavior becomes increasingly modified. The behavior of juvenile marmots in this study supports this idea; juveniles are more likely to be preyed upon than are older animals (Holmes 1979, Carey 1983) and they showed the greatest number of significant correlations between usage indexes and habitat characteristics related to predator detection.

Juveniles may also need to balance the conflicting demands of feeding and predator avoidance to a greater extent than do older animals because of their higher sensitivity to reductions in feeding rate (Sih 1982). The relatively small amount of time available for weight gain between emergence from natal burrows and entrance into the first hibernation period reduces the amount of feeding time available for juveniles relative to yearlings and adults (Armitage et al. 1976). Juveniles have additional nutrient requirements for growth, which reduces the amount of assimilated energy that can be stored as fat. These constraints on feeding are reflected in juvenile behavior, which showed the strongest relationships between foraging area preferences and food availability. A further indication that nutrient intake was an important determinant of juvenile foraging patterns is that the only significant correlation found between Trifolium biomass and usage indexes was for juvenile data. This forb is high in protein and low in fiber content which makes it an easily digestible and nutritious food item (Carey 1983).

The foraging behavior of parous females was also influenced by food availability and, to a lesser degree, predator avoidance. Reproductive females typically do not begin depositing fat for hibernation until weaning their litters (Andersen et al. 1976); nutrient intake may therefore have a strong influence on foraging for them as well. Because no nonparous adult females were observed in the present study, conclusions regarding the effect of reproductive state on foraging area selection could not be made (see Barash 1980).

Examination of risks imposed on yearlings further supports the conclusions drawn for juveniles and for parous females. With as yet no reproductive demands to support, yearlings are able to divert a large portion of their energy intake into fat storage for hibernation. In addition, greater familiarity with their surroundings and predators may reduce predation risk for yearlings relative to juveniles. It is possible that other variables not measured in this study (e.g., aspects of the social structure of the colony) may be more influential than food or predators in shaping foraging patterns of yearlings. Yellow-bellied marmots typically disperse or remain in their natal colony during their second summer, and it appears that the ´choice´ is related to social and demographic parameters in the natal colony during this time (Downhower and Armitage 1981).

In conclusion, the results presented here indicate that yellow-bellied marmots forage in a variety of microhabitat types but spend greater amounts of time in areas that afford both abundant food and a wide visual field for predator detection. Food availability is the primary habitat characteristic associated with foraging area preference by adult females and, to a lesser degree, yearlings. Both food availability and predator avoidance influence foraging movements of juveniles. These relationships reflect differential vulnerability to predation and to the consequences of inadequate nutrient intake among marmot age classes.

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Table 1. Habitat characteristics of foraging areas used by marmots in MacAfee Meadow, White Mountains, California. Data were collected during July and August 1982.

	Foraging areas										
Variable	1	2	3	4	5	6	7	8	9	10	11
Distance to home burrow (m)	80.0	160.0	28.0	180.0	100.0	80.0	90.0	150.0	110.0	100.0	40.0
Relative size (%)	5.7	10.9	14.3	5.1	2.3	6.9	9.1	9.1	5.1	11.4	20.0
Soil moisture (%)	11.6	7.8	8.6	32.2	21.2	33.7	7.8	6.5	29.9	22.6	32.3
Vegetation height (cm)	12.8	16.5	14.2	16.4	16.2	18.4	15.8	14.6	21.0	15.4	26.2
Safety burrow density (burrows/1000 m^2)	7.0	6.0	5.0	9.0	10.0	4.0	9.0	9.0	3.0	8.0	3.0
Food biomass (g/m^2)*	141.0 224.0	121.0 95.0	124.0 235.0	20.0 34.0	77.0 61.0	6.0 47.0	103.0 119.0	118.0 263.0	22.0 39.0	82.0 145.0	1.0 29.0
Koeleria biomass (g/m^2)*	70.0 179.0	58.0 67.0	84.0 219.0	8.0 0.0	20.0 11.0	4.0 22.0	55.0 90.0	58.0 224.0	12.0 0.0	4.0 90.0	0.0 11.0
Trifolium biomass (g/m^2)*	66.0 23.0	94.0 23.0	33.0 18.0	0.0 0.0	37.0 3.0	0.0 5.0	45.0 28.0	57.0 31.0	0.0 1.0	70.0 32.0	0.0 2.0
Haplopappus biomass (g/m^2)*	2.4 14.0	2.4 2.8	0.9 2.1	0.6 18.0	15.6 45.0	1.8 14.0	0.6 1.4	0.0 7.0	6.6 18.0	4.2 7.0	0.0 1.8
Vegetation volume (% x cm)*	3.0 4.0	3.3 4.1	5.3 5.8	3.9 4.9	4.2 7.8	13.4 14.0	6.9 5.2	6.7 5.7	13.4 14.3	2.3 3.9	16.8 12.8
Vegetation cover (%)*	0.55 0.66	0.59 0.63	0.64 0.53	0.65 0.93	0.89 0.90	0.97 0.98	0.61 0.66	0.65 0.59	0.92 0.92	0.77 0.88	0.94 0.96

* Upper values are data collected in period 3; lower values were collected in period 4.

Table 2. Foraging area use by yellow-bellied marmots during midsummer (7 July - 15 August). Ranks of usage indexes° are shown in parentheses. P=preferred, L=less preferred, N=neutral based on contributions to total chi square value (see text for further explanation).

Area	All Animals	Juveniles	Yearlings	Adults
1	(11) P	(10) P	(11) P	(11) P
2	(9) P	(11) P	(8.5) N	(10) P
3	(10) P	(8) N	(10) P	(9) N
4	(6) P	(7) P	(1.5) L	(5) P
5	(3) P	(4) P	(1.5) N	(3) P
6	(5) N	(3) L	(8.5) P	(6) N
7	(8) N	(5) L	(7) L	(8) N
8	(7) N	(9) P	(6) L	(7) N
9	(2) L	(1) L	(4) L	(4) N
10	(4) L	(6) L	(5) L	(2) L
11	(1) L	(2) L	(3) L	(1) L

° Usage index=number of sightings of marmots feeding in an area divided by the total number of sightings for all areas.

Table 3. Spearman rank correlation coefficients between indexes of foraging area use and habitat variables in midsummer (7 July-15 August).

Variable	All animals	Juveniles	Yearlings	Adults
Food biomass	0.846**	0.809**	0.699*	0.800**
Food cover:total vegetation cover	0.809**	0.782*	0.589	0.773**
Koeleria biomass	0.813**	0.717*	0.624*	0.845**
Trifolium biomass	0.586	0.730*	0.421	0.447
Haplopappus biomass	-0.124	-0.128	-0.037	-0.082
Soil moisture	-0.656*	-0.683*	-0.396	-0.620*
Total vegetation cover	-0.898**	-0.847**	-0.542	-0.811**
Vegetation height	-0.673*	-0.673*	-0.502	-0.546
Vegetation volume	-0.515	-0.711*	-0.185	-0.310
Safety burrow density	0.235	0.363	-0.273	0.078
Distance to sleeping burrows	0.014	0.251	-0.431	-0.027

* $P \leq .05$; ** $P \leq .01$

Table 4. Factor loadings for habitat variables measured in midsummer (7 July - 15 August). See text for description of variables and interpretation.

	Factor Loadings	
Variables	1	2
Food biomass	0.958	0.000
Food plant cover: vegetation cover	0.912	0.258
Koeleria biomass	0.913	0.000
Trifolium biomass	0.810	0.277
Soil moisture	-0.942	0.000
Total vegetation cover	-0.918	0.000
Vegetation height	-0.770	-0.437
Vegetation volume	-0.705	-0.613
Haplopappus biomass	-0.280	0.793
Safety burrow density	0.407	0.732
Cumulative proportion of variance explained	0.667	0.824

Table 5. Spearman rank correlations between foraging area usage indexes and factor scores.°

	Factors	
Age class	1	2
Mid summer		
All marmots	0.909**	0.073
Juveniles	0.918**	0.345
Yearlings	0.662*	-0.045
Adults	0.836**	-0.301
Late summer		
All marmots	0.797**	0.223
Juveniles	0.714*	0.405
Yearlings	0.473	-0.236
Adults	0.845**	0.191

* $P \leq .05$; ** $P \leq .01$

° Factor scores are from factor analysis as explained in methods.

APPENDIX A

Hourly Activity Budgets of Yellow-bellied Marmots in the White Mountains of California

To quantify the time marmots spent in various behaviors on an hourly basis observations were conducted between 5 July and 30 August 1982 on members of the colony studied in the White Mountains of California (Chapters 1-3). Individual marmots were observed for 2-hour sample periods during the peak foraging times (0600-1000 h, 1500-1700 h). During each sample period the behavior of the marmot was recorded at 5-minute intervals and categorized as 1 of 8 mutually exclusive behavioral states. Sample points in which the marmot was out of the observer's view and its behavior was unknown were categorized as 'out of sight'. To calculate the percentage of time spent in each behavior, the frequency of each behavioral category was divided by the total number of observation points for each sample (24) and multiplied by 100. nineteen samples were obtained from 13 different individuals (5 adults, 2 yearlings and 6 juveniles); mean percentages over all samples are given with standard errors in parentheses.

Description of behavioral categories	
Foraging:	Ingesting or searching for food with the head down
Sunning:	Lying flat, usually on a rock, with legs extended and head low
Social : interaction	Interacting, either amicably or agonistically, with another marmot
Alert:	Sitting with head up or standing on hind legs, looking out
Nesting:	Gathering grass in mouth for transport to burrow
Moving:	Walking or running from one point to another (does not include movement during feeding)
Grooming:	Grooming of own body (licking, scratching, etc.)
In burrow:	Applies to time when observer knows with certainty that the focal animal is underground.

Behavior	Mean % of time (s.e.)
Foraging	60.1 (4.4)
Sunning	4.7 (1.5)
Social interaction	1.7 (0.7)
Alert	7.6 (2.4)
Nesting	0.2 (0.0)
Moving	6.5 (1.7)
Grooming	0.5 (0.4)
In burrow	6.6 (2.8)
Out of sight	11.5 (3.0)

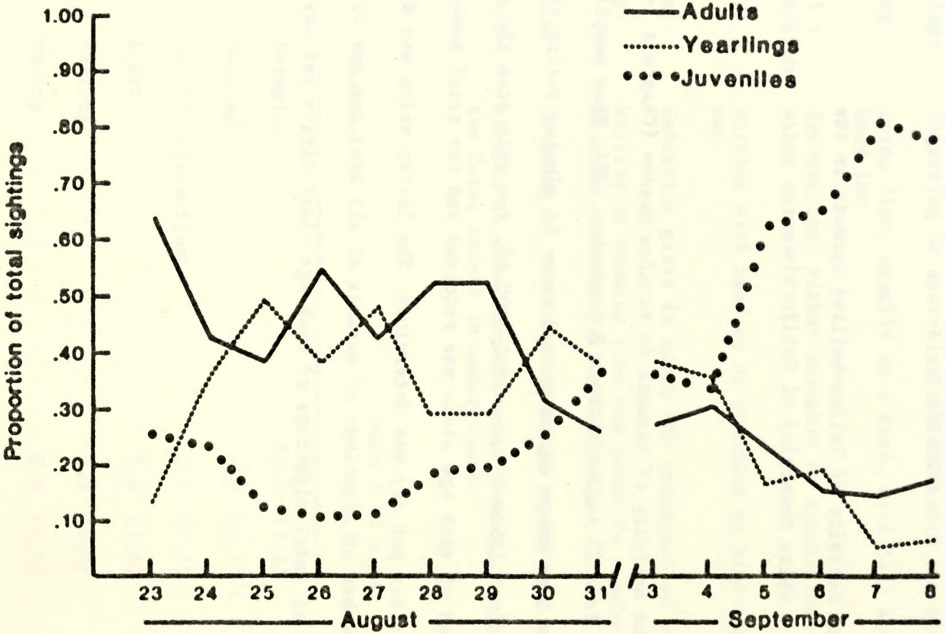
APPENDIX B

Late Season Activity of Yellow-bellied Marmots in the White Mountains of California

Methodolgy

Late-season activity of marmots in MacAfee Meadow (Chapters 1-3) was determined from 23 August through 8 September 1982. Scan sampling of the colony's home range was conducted every 15 minutes during the peak foraging times (0600-1000 h, 1500-1900 h). For each scan the number of sightings of each age class was recorded and the total number of sightings per class per day was determined. The latter value was divided by the total number of sightings of marmots of all ages per day to give the proportion of total sightings of each age class active per day.

Appendix B: Late summer activity of marmots in the White Mts



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